

THE NATURE AND SIGNIFICANCE OF NON-RECIPROCAL FERTILITY IN
Aedes scutellaris AND OTHER MOSQUITOES.

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(Three Text-figures.)

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Synopsis.

When crosses are made between two subspecies of *Aedes scutellaris*, the matings prove fertile or infertile according to the direction in which the matings are made. In the mating of subsp. *scutellaris* (S) females with subsp. *katherinensis* (K) males, fully viable eggs are produced. In the reciprocal mating, copulation, insemination and egg laying are normal, but the eggs are totally inviable.

This non-reciprocal fertility shows strictly maternal inheritance. Backcrosses of F_1 females to subsp. *katherinensis* males are viable and the B_1 progeny are of *scutellaris* mating type. In successive backcrosses to *katherinensis* males, to the B_0 generation, the *scutellaris* mating type is retained. B_{0k} males, derived from repeated backcrosses to subspecies *katherinensis*, are still incompatible with *katherinensis* females.

The genetic system determining the inheritance of mating type must depend either on anomalous meiosis in oogenesis or on nucleus-independent cytoplasmic factors. There is no critical evidence enabling a choice between these two hypotheses.

A survey of the available data on non-reciprocal fertility between species, subspecies, and races of *Aedes* and *Culex* suggests that it has had significance as a source of incipient speciation in mosquitoes.

INTRODUCTION.

The natural history of mosquitoes has long held a place of importance in entomological research, and the systematics of the Culicidae has advanced to a stage where the limits between species are often finely drawn on the bases of morphological, physiological and ecological criteria. The application of the genetic concept of species, which emphasizes intrinsic isolation, is likely to cause some reorientation of the taxonomy of the group in the near future.

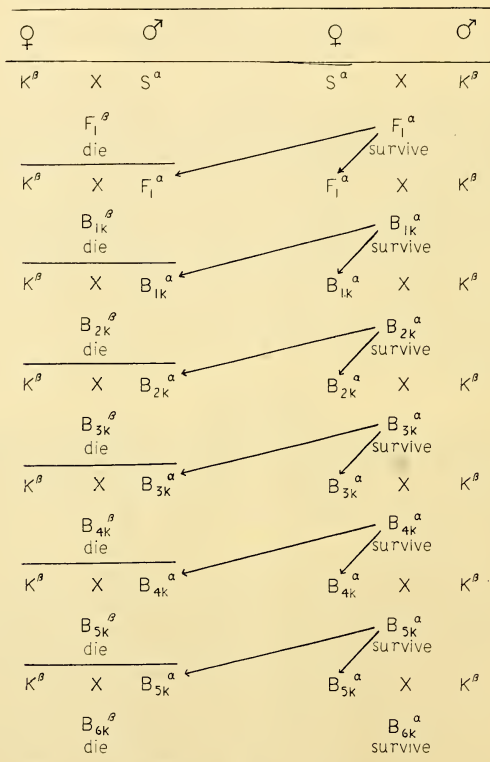
The isolating mechanisms which exist between closely allied species include a range of types similar to those known in *Drosophila*. They may be genetic, mechanical, ecological, physiological, or behaviouristic in nature. Such isolating mechanisms usually operate in both reciprocal directions between males and females of the species concerned. Differences in fertility between reciprocal crosses, however, are known to occur between races, subspecies or species in several genera (Toumanoff, 1939, 1950; Downs and Baker, 1949; Bonnet, 1950; Perry, 1950; Woodhill, 1949, 1950; Marshall, 1938; Laven, 1951, 1953; Dobrotworsky and Drummond, 1953) and it is apparent that the phenomenon is widespread in the Culicidae. It has introduced difficulties and complexities in the appreciation of specific and subspecific categories, and it has a significant bearing on problems of medical entomology. It is also significant to genetical and evolutionary theory. Its mechanics must depend on a uniparental genetic system, and its role in the origin of intrinsic species barriers is problematical.

THE MATERIAL.

Aedes scutellaris Walker belongs to a species-complex which includes a number of species, subspecies and geographical races of doubtful rank. Many of the forms show complete intrinsic isolation, and undoubtedly deserve specific status. A peculiar non-reciprocal fertility was described by Woodhill (1949, 1950) in crosses between two subspecies, *A. scutellaris scutellaris* Walker and *A. scutellaris katherinensis* Woodhill. Complete fertility was found when subsp. *scutellaris* females and subsp. *katherinensis* males were mated, but hybrid eggs from the reciprocal cross were totally inviable. This

mating incompatibility was found to extend to the backcrosses to *katherinensis*. Smith-White (1950) drew attention to the possible genetic and evolutionary significance of the phenomenon, and suggested a backcross program which might clarify its nature.

The original isolation of subsp. *katherinensis* was obtained from Katherine, in the Northern Territory, in January, 1948, and consisted of a batch of eggs from an unknown number of females. This isolation has been maintained in the laboratory under the culture designation "K". An isolation of subsp. *scutellaris* was obtained from New Guinea at about the same time, and has been maintained as culture "S".



Text-figure 1.—The Backcross Program.

S = *A. scutellaris scutellaris*; K = *A. scutellaris katherinensis*; α and β represent maternally inherited factors, affecting survival. They may be carried either in the cytoplasm or in the nuclei.

In April, 1953, Mr. K. O'Gower obtained eggs from eleven females of subsp. *katherinensis* at Batchelor, 126 miles north-west of Katherine. This new isolation, designated culture "B", is morphologically identical with the Katherine material, and shows an identical behaviour when crossed with subsp. *scutellaris*. In the cross S × B, 3200 F₁ eggs yielded 2495 larvae (77.9% hatch), but in the reciprocal cross B × S, 2514 eggs were totally inviable. *A. scutellaris katherinensis* possesses a wide geographical distribution in northern Australia, and it can be distinguished from the type subspecies by morphological criteria.

Aedes scutellaris is a less satisfactory laboratory subject than is *Culex molestus*. It requires warm temperatures and high humidity, which necessitate special culture rooms. Blood-feeding is necessary before egg-laying, and matings are only successful when large numbers of the two sexes are confined in the breeding cages. The eggs are laid singly, and the progeny of individual females cannot easily be isolated from the mass mating cages.

THE BREEDING PROGRAM.

The main part of the breeding program has consisted of a series of backcrosses to test for permanence or breakdown of incompatibility with K females. Data on sex ratio in cultures, and of F_2 segregation for a morphological character "white line", are reported. An inbreeding program with culture S was commenced for the isolation of possible recessive genes, but has been abandoned temporarily.

All larval cultures were maintained in incubators at 27°C. and matings were made in muslin cages measuring 10" × 10" × 12", in a warm room at 27°C. and 75-80% relative humidity.

The backcross data. Three series of backcrosses have been made. The first series commenced with the F_1 hybrids produced by Woodhill (1950), and was continued to the fifth backcross generation (Text-figure 1 and Table 1). In the Text-figure, and in Tables

TABLE 1.
The First Backcross Experiment.

	Cross.	Progeny Designation.	Eggs Laid.	Eggs Hatched.	Percentage Hatch.
1	$K^\beta \times S^\alpha$	F_1^β	—	—	0
2	$S^\alpha \times K^\beta$	F_1^α	—	—	high
3	$F_1^\alpha \times S^\alpha$	B_{1s}^α	650	normal	high
4	$S^\alpha \times F_1^\alpha$	B_{1s}^α	1150	normal	high
5	$F_1^\alpha \times K^\beta$	B_{1k}^α	480	normal	high
6	$K^\beta \times F_1^\alpha$	B_{1k}^β	1220	0	0
7	$B_{1k}^\alpha \times K^\beta$	B_{2k}^α	normal	normal	ca 90
8	$K^\beta \times B_{1k}^\alpha$	B_{2k}^β	2000	13	0.65
9	$B_{2k}^\alpha \times K^\beta$	B_{3k}^α	normal	normal	ca 90
10	$K^\beta \times B_{2k}^\alpha$	B_{3k}^β	4800	12	0.25
11	$B_{3k}^\alpha \times K^\beta$	B_{4k}^α	normal	normal	ca 90
12	$K^\beta \times B_{3k}^\alpha$	B_{4k}^β	4200	58	1.38
13	$B_{4k}^\alpha \times K^\beta$	B_{5k}^α	normal	normal	ca 90
14	$K^\beta \times B_{4k}^\alpha$	B_{5k}^β	4600	84	1.87
15	$B_{3k}^\beta \times K^\beta$	B_{4k}^β	not recorded		over 90
16	$K^\beta \times B_{3k}^\beta$	B_{4k}^β	not recorded		over 90

1-3, the backcross formulae require brief explanation. The subscripts indicate the generation, B_{3k} being the third backcross to K after the F₁, and the superscripts indicate the "maternal line" of each family, and are significant for any cytoplasmic or nuclear factors having a strictly maternal inheritance. B_{3k}^α is the third backcross to K, tracing its maternal ancestry back to the original S stock, B_{3k}^β has had the K maternal line introduced.

TABLE 2.
The Second Series of Backcrossing.

Serial No.	Cross.	Progeny Designation.	Numbers Mated.		Eggs Laid.		Hatch.	
					Total.	%	Total.	%
1	S ^α selfed	S ^α	48	100	2022	42.1	1450	71.1
2	K ^β selfed	K ^β	104	76	2104	20.2	1583	75.3
3	S ^α × K ^β	F ₁ ^α	56	62	2482	44.3	1499	60.4
4	K ^β × S ^α	F ₁ ^β	126	202	3390	27.0	0	0.0
5	F ₁ ^α × F ₁ ^α	F ₂ ^α	135	205	3534	26.2	863/1254	68.7
6	F ₁ ^α × S ^α	B _{1s} ^α	86	126	2006	23.3	320/573	55.8
7	S ^α × F ₁ ^α	B _{1s} ^α	164	150	9218	56.2	686/748	91.7
8	F ₁ ^α × K ^β	B _{1k} ^α	112	126	2589	23.1	1647	63.6
9	K ^β × F ₁ ^α	B _{1k} ^β	91	103	1767	19.4	0	0.0
10	B _{1k} ^α × K ^β	B _{2k} ^α	82	68	1892	23.1	1340	70.7
11	K ^β × B _{1k} ^α	B _{2k} ^β	51	113	1408	27.6	0	0.0
12	B _{2k} ^α × K ^β	B _{3k} ^α	59	73	1618	27.2	1051	64.8
13	K ^β × B _{2k} ^α	B _{3k} ^β	88	56	1254	14.3	0	0.0
14	B _{3k} ^α × K ^β	B _{4k} ^α	77	91	1831	23.8	1072	58.6
15	K ^β × B _{3k} ^α	B _{4k} ^β	92	92	1567	17.0	0	0.0
16	B _{4k} ^α × K ^β	B _{5k} ^α	71	98	1573	22.2	1083	68.7
17	K ^β × B _{4k} ^α	B _{5k} ^β	75	102	1564	20.8	0	0.0
18	B _{5k} ^α × K ^β	B _{6k} ^α	78	86	1654	21.2	989	60.5
19	K ^β × B _{5k} ^α	B _{6k} ^β	69	68	1372	19.9	0	0.0

The first series of backcrosses show a slight breakdown in the inviability of K-line hybrid eggs, in the B_{2k}^β generation, and there is a slight but very doubtfully significant increase in breakdown in the later generations. Breakdown individuals possessed complete fertility with the K parental stock in both reciprocal directions, but were not tested against the S stock. These results parallel those obtained by Laven (1953). Since